TORREYA

May, 1913.

Vol. 13 No. 5

THE VEGETATION OF CONNECTICUT

I. PHYTOGEOGRAPHICAL ASPECTS

BY GEORGE E. NICHOLS

From a taxonomic standpoint the flora of Connecticut is adequately summed up in the several more or less comprehensive bulletins which have been published by the Connecticut Geological and Natural History Survey,[1] but except for a few casual references which have appeared incidental to these and other papers no attempt has yet been made to portray the ecological relations. With the intent of supplying in a measure this deficiency the writer has undertaken a study of the vegetation of the state from an ecological point of view, the results of which are to be presented in this and subsequent papers. Although much of the work has necessarily been in the nature of a reconnaissance, and while many of the observations set forth will already be familiar to some of the readers, it is felt, nevertheless, that some such preliminary survey of the field in question is essential as a basis for future research. In this first paper attention is directed principally to those larger and more general aspects of plant distribution which seem of phytogeographical interest. The discussion of plant societies, successional relations, and other problems of a more distinctly local nature is deferred until later.

[1] Evans & Nichols, The bryophytes of Connecticut, Bull. 11, 1908; Graves, Eames, Bissell, Andrews, Harger, & Weatherby, Catalogue of the flowering plants and ferns of Connecticut, Bull. 14, 1910. Bulletins 3, 5, 10, and 15 deal with algae and fungi.

[No. 4, Vol. 13, of TORREYA, comprising pp, 73–88 was issued 6 April 1913.]

By way of introduction the status of the flora from a qualitative viewpoint may be briefly summarized. Exclusive of the thallophytes, 1,949 indigenous species of plants have been recorded from Connecticut. Of these the bryophytes include 463 (liverworts 134, mosses 329), the pteridophytes 74, and the spermatophytes 1,412 (gymnosperms 13, monocotyledons 496, dicotyledons 903). Besides the native element there is a large and constantly increasing number of spermatophytes which have been variously introduced and which in many cases have become thoroughly established. Upward of 460 such aliens are now known, but while qualitatively and even quantitatively abundant, they may largely be disregarded in the present discussion, since they serve to complicate rather than simplify matters. Nearly 70 per cent of the indigenous plants are endemic to North America, the remaining 30 per cent being in large part common to Europe or Asia or both. It is instructive to note, however, how vastly the relative proportions of endemic and extra-continental species vary among and within the great divisions and subdivisions of the plant kingdom. For while less than 20 per cent of the local bryophytes are endemic, and of the pteridophytes hardly 50 per cent, fully 92 per cent of the gymnosperms (*Juniperus communis* seems to be the sole exception), 80 per cent of the monocotyledons, and nearly 90 per cent of the dicotyledons are not known to occur outside of this continent. Furthermore, among the pteridophytes, for example, only 30 per cent of the homosporous species but nearly 80 per cent of the heterosporous species are endemic; and similarly among the dicotyledons, to select specific cases, it would seem that while nearly 30 per cent of the 37 local Ranunculaceae are extra-continental in range, all but about 2 per cent of the more than 160 Compositae are endemic. The general assertion may be made that in the more primitive groups of plants the species tend to have a wider range than in the more advanced groups; or, to use a different phraseology, that species in groups of comparatively recent evolutionary derivation are far more restricted in range than species in groups of more ancient origin. An examination of the intra-continental ranges of the various species which comprise

the local flora also brings to light certain suggestive distributional peculiarities. It is found that while the majority of the species which are known to occur in Eurasia, range far to the north on this continent, the endemic species exhibit decidedly southward tendencies. For example, of the 28 endemic Ranunculaceae native to Connecticut, only 5—about 18 per cent—have been recorded north of New England or Nova Scotia, while at least 5 —in this case more than 50 per cent—of the 9 extra-continental species have a more or less boreal distribution. Similarly, among the bryophytes 84 per cent of the endemic species are apparently confined to latitudes south of northern New England.

In themselves statistics like these may be interesting, but it is only as they offer some intimation regarding the history and relationships of the flora that they become of any great value. In common with other glaciated regions the modern era of plant life in Connecticut dates back to the period when the continental glaciers receded toward the pole. In order, however, to clearly apprehend not only the origin of the native flora but also its affinities to that of other regions one must journey back to preglacial times. For an extended period during the lower Tertiary there must have existed greater or less continuity between the continental land masses of the northern hemisphere, and during at least a portion of that time the climate in the present subarctic regions must have been sufficiently mild to permit the circumpolar migration of temperate plants. In this and no other manner can the undeniable similarity of certain components, notably the bryophytes, in the vegetation of Europe and North America be accounted for. But with the advent of the climatic changes which caused or accompanied the development of the continental ice sheet great transformations in the vegetation were induced. As the glaciers advanced southward the temperate plants, unable to withstand the more rigorous atmospheric conditions, slowly retreated, their places being seized progressively by arctic species which during the warmer period of the early Tertiary had apparently been confined to extreme polar regions. The southward margin of the continental ice sheet in the eastern United States is marked by the terminal

moraine which now forms a part of the "backbone" of Long Island, reaching thence westward through Staten Island and northern New Jersey. The entire state of Connecticut was buried beneath an immense accumulation of ice and snow and its vegetation completely annihilated.

As shown by the terminal moraines on Long Island there were at least two distinct glacial epochs in this region. It was during the first of these, when practically the entire northern half of the island was ice-bound, that the southernmost (Ronkokoma) moraine was formed and the broad outwash-plain which today obscures most of the Cretaceous substructure of the southern half of the island was largely developed. At the time of maximum glaciation, when the building up process must have been most actively progressing, it is doubtful whether vegetation could have maintained any appreciable foothold on the shifting surface of southern Long Island. But with the stability that ensued upon the temporary withdrawal of the ice the soil doubtless became populated rapidly by plants which pressed in from the unglaciated regions farther south and, although it is impossible to determine accurately just what conditions obtained in the period which intervened between the temporary retreat and the subsequent reencroachment of the ice sheet, it seems not unlikely that the vegetation came to assume much the same aspect that it exhibits today. If so, upon the readvancement of the ice temperate plants were once more superseded by arctic forms and it may safely be assumed that in the southern part of the island these persisted throughout the reign of cold that followed. With this latter hypothesis in mind one can picture, in the imagination, the floristic aspect of Long Island during this last period of glaciation. The northern edge of the island is buried under a vast sea of ice which stretches monotonously poleward. Between the glacier's margin and the old Ronkokoma moraine to the south there is scant opportunity for plant life to become established on account of the instability of the rapidly upbuilding outwash-plain. But south of the Ronkokoma moraine the surface of the plain is clothed with a low, dense carpet of vegetation similar to that found in the Alaskan tundra of

today. Owing to the fact that even during the summer it never thaws to any depth the ground is wet and boggy. Sphagnums, Cladionas, and Polytrichums abound, while here and there are seen scattered clumps of shrubs—*Chamaedaphne*, *Andromeda*, *Ledum*, *Betula pumila*, *Myrica Gale*, *Alnus incana*, and the like—interspersed with such forms as *Vaccinium Oxycoccus*, *Potentilla palustris*, *Chiogenes*, *Drosera*, *Menyanthes*, *Scheuchzeria*, *Eriophorum*, *Cyperus*, and other sedges. Upon the higher levels, and perhaps upon the moraine itself, there may be groups of trees—firs, spruces, and tamaracks—but nowhere is there the faintest resemblance to the present day vegetation of the Long Island uplands. Such a picture is admittedly fanciful, but to the mind of the writer it approximates the actual conditions which must have prevailed at that time.

The final withdrawal of the glaciers from this region left the topography of Long Island and Connecticut in much the condition that now exists. As the ice front retreated northward there doubtless followed immediately in its wake, wherever soil conditions were suitable, such a tundra formation as the one depicted above, with the advance guard of the coniferous forest, which was destined to occupy temporarily the freshly exposed land areas, but with a few miles in the rear. With the gradual reëstablishment of a milder climate and the contemporaneous thawing and drainage of the ground, which proved fatal to the tundra vegetation, the environment once more became suitable for a temperate flora, and an invasion of plants from the south was inaugurated. In the struggle for the possession of the new territory which must have ensued when these southern invaders began their march northward the boreal element for a time doubtless maintained its own. But partly as a result of decreased vitality under the changed climatic and soil conditions the arctic flora was unable to cope successfully with the more vigorous and adaptable temperate vegetation, so that eventually it was in large part either exterminated or forced northward, with the exception of a relatively small number of forms which had taken refuge, figuratively speaking, in bogs where their descendants still survive.

In the light of these observations it clearly follows that while practically all of the species which at present comprise the flora of this state have been derived directly from the south, nevertheless many of them—certainly those which today are common to Europe—must have existed in preglacial times not only here but far to the north. Of the forms which are now endemic to North America many, like the tulip tree, sweet gum, and sassafras, are known to have been native to Europe in preglacial time, their extinction there being accounted for by assuming that they were trapped, as it were, between the advancing glaciers toward the north and insurmountable east-west mountain ranges toward the south and thus wiped out of existence. But it is equally certain that a large share of these endemic species have never occurred in Europe, and for such species there are two alternative possibilities: either they must have attained their present evolutionary development since the discontinuance of the circumpolar land bridge, or else they must have been restricted until within comparatively recent times to the warmer parts of this continent, so that the opportunity to migrate into Europe has never been afforded them.

The present distribution of the vegetation within the state is the effect of a complex of causes, some of which have long since ceased to operate while others are still active. To a large extent coeval factors of topography, soil, and climate seem ample to explain the observed relations. But there is one problem of plant distribution for which coexistent forces fail to offer any satisfactory solution. This problem relates to the segregation in the southeastern part of Connecticut of a remarkable group of plants which are characteristic of the Atlantic coastal plain region from Long Island and New Jersey southward.[1] The majority of the species involved also range eastward into Rhode Island and southeastern Massachusetts, some of them following

[1] In order, however, to avoid any misapprehension it should be remarked that very many coastal plain plants are more or less widely distributed through the state. A comparison, for example, of the Connecticut catalogue of ferns and flowering plants with Stone's Plants of southern New Jersey (Ann. Rept. N. Jersey State Mus., 1910) shows that nearly 75 per cent of the 540 species listed as characteristic of the New Jersey coastal plain are also found in this state.

the coast northward into the southern parts of Maine and New Hampshire, and a few reaching as far north as Nova Scotia, New Brunswick, and even Newfoundland. The following list comprises coastal plain species which in this state have been found only east of the Connecticut River.[1]

*Sphagnum macrophyllum**†
*Sagittaria longirostra**
Sagittaria Engelmanniana
*Paspalum psammophilum**†
Paspalum circulare†
*Panicum virgatum cubense**†
*Panicum spretum**†
*Panicum oricola**†
Panicum auburne
*Eleocharis Torreyana**
*Carex albolutescens**†
*Carex nigro-marginata**†
Carex ptychocarpa
*Carex bullata**
*Juncus effusus conglomeratus**
*Desmodium sessilifolium**
*Hypericum adpressum**†
*Myriophyllum scabratum**†
*Schwalbea americana**
*Aster spectabilis**†

In the same category should be included two other groups of coastal plain plants. The first is made up of species whose distributional area in the state obviously centers in the southeast but which may extend for some distance westward along the coast or northwestward into the valley of the Connecticut River. Worthy of mention among such forms are:

*Calypogeia Sullivantii**†
*Panicum Commonsianum**†
*Panicum Addisonii**
*Eleocharis tuberculosa**
*Scleria pauciflora**
*Juncus militaris**†
*Xyris Smalliana**†[1]
*Lachnanthes tinctoria**†
*Ilex opaca**†
*Ilex glabra**†
*Ludvigia sphaerocarpa**†[2]
*Sabatia dodecandra**†
*Asclepias variegata**†
*Scutellaria integrifolia**†
*Plantago elongata**†
*Eupatorium aromaticum**†
*Gnaphalium purpureum**†

[1] In this and the two succeeding lists the asterisk (*) and dagger (†) indicate that a species is recorded from the New Jersey coastal plain and Long Island respectively.

[2] In Connecticut known only from West Pond, Guilford, but also found in eastern Massachusetts.

The other group embraces plants which occur locally in other parts of the state but which for the most part are frequent or common in the southeastern section. Representative of this assemblage are:

*Chamaecyparis thyoides**†
*Rynchospora macrostachya**†
*Aletris farinosa**†
*Leucothoë racemosa**†
*Gaylussacia frondosa**†
*Rhododendron maximum**†
*Arctostaphylos Uva-ursi**†[1]
*Nymphoides lacunosum**†
*Lycopus sessilifolius**†
*Utricularia inflata**†
*Utricularia purpurea**†

It is hardly necessary to consider individually the distribution of the various species mentioned above. As the only arborescent form referred to, *Chamaecyparis thyoides*—the coast white cedar—may be selected as fairly typifying in its range the whole group. This tree, in common with all of the plants mentioned, except *Arctostaphylos*, is endemic to North America. South of New England it ranges from Mississippi northward into Long Island being practically confined to the coastal plain. Thence it extends through Connecticut, Rhode Island, and eastern Massachusetts as far north as southern New Hamsphire, and it is also reported as "doubtfully indigenous in Nova Scotia."[2] The coast white cedar usually grows in swamps where it forms colonies of wonderful density, averaging a greater number of trees per acre than any other native species (Fig. 1.) Such "cedar swamps" are of frequent occurrence in southern New Jersey and in parts of Long Island and southern New England, sometimes covering more than a thousand acres. In eastern Connecticut, as farther south, the great laurel (*Rhododendron maximum*) often forms a luxuriant, almost impenetrable tangle of undergrowth. In connection with the present problem the writer has gone to considerable effort in an attempt to secure as exact information as possible regarding the distribution of these cedar swamps, past or present, in Con-

[1] Not a southern species but one of the most characteristic plants of the New Jersey pine-barrens. In southeastern Connecticut, as in New Jersey, it often forms a veritable carpet over the sandy soil.

[2] Gray's Manual, ed. 7, p. 66.

necticut and southern New York, and the results of the investigation are graphically shown on the accompanying map (fig. 2). It will be seen that there is an almost continuous chain of them extending the length of Long Island, and it is anticipated that further exploration may supply the missing links in the series.

FIG. 1. Interior of cedar swamp at Ledyard. *Chamaecyparis thyoides* and *Rhododendron maximum.*

Doubtless there were formerly cedars in the swamps of Staten Island, but these apparently have long since been obliterated. The cedar has also been found on Plum Island—one of the hiatus-like islands which are intercalated between the eastern end of Long Island and the mainland, while in Connecticut their abundance in the eastern and scarcity in the western part of the state is obvious.

The problem as to the origin or cause of this unique flora in southeastern Connecticut and eastward is one of unusual interest. So far as known there are no pronounced climatic dissimilarities to which it can be attributed, neither is there at present any evidence of topographic or soil conditions sufficiently diverse from those in other parts of the state to afford an adequate explanation. The most satisfactory solution seems to rest on the assumption that in post-glacial time there has been a land bridge which connected eastern Long Island with the adjacent mainland and across which northbound coastal plants could readily pass without entering western Connecticut. The probability that such a formation once existed was urged by Hollick in 1893[1] as an explanation for the occurrence of certain coastal plain plants in Rhode Island and southeastern Massachusetts, and Fernald has recently[2] brought forward convincing botanical evidence in the light of which it seems not improbable that for some time after the recession of the glaciers a more or less continuous land connection stretched northward as far as Newfoundland. In view of the extended discussion of this hypothesis in these papers no further comment is called for here. It must be admitted, however, that the isolation in southeastern Connecticut of such an appreciable colony of coastal plain plants, 75 per cent of which are common both to Long Island and New Jersey, affords strong confirmation of the views advanced by Hollick and Fernald. It is especially difficult to conceive how the coast white cedar could have migrated eastward through southwestern

[1] Plant distribution as a factor in the interpretation of geological phenomena, with special reference to Long Island and vicinity, Trans. N. Y. Acad. Sci., 12: 189–202. 1893.

[2] A botanical expedition to Newfoundland and Labrador, Rhodora 13: 109–162. 1911.

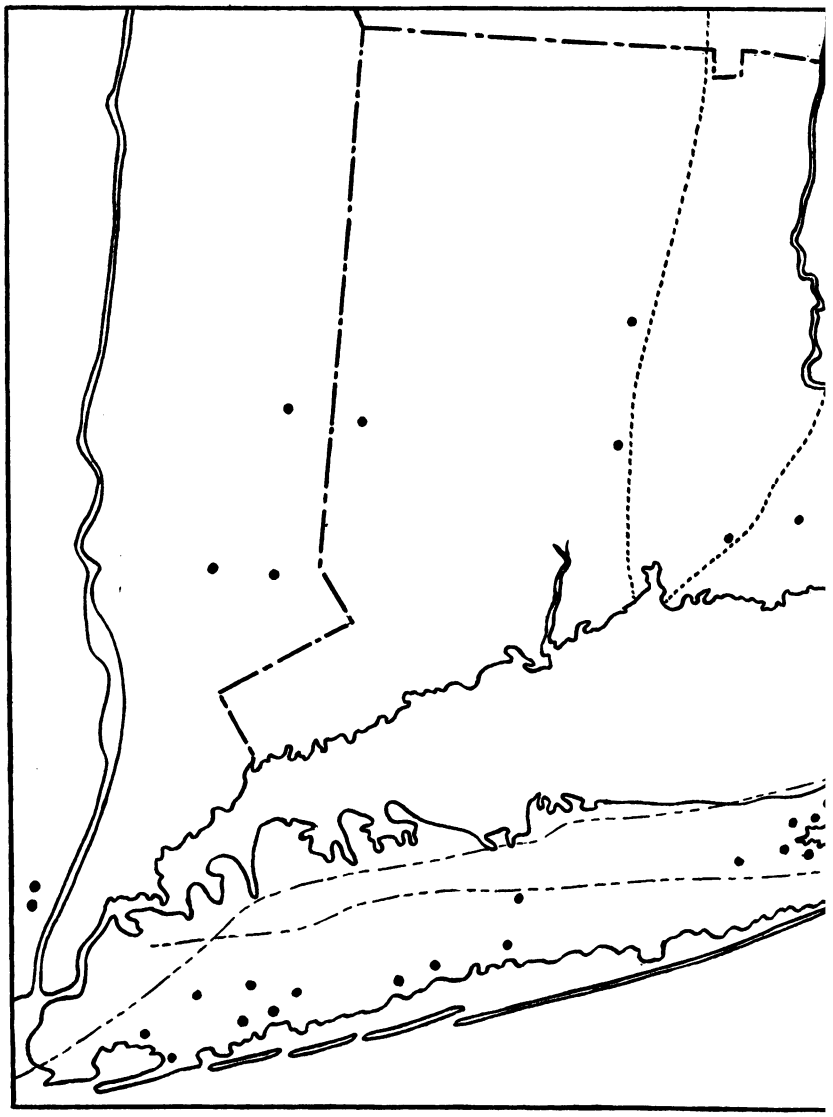
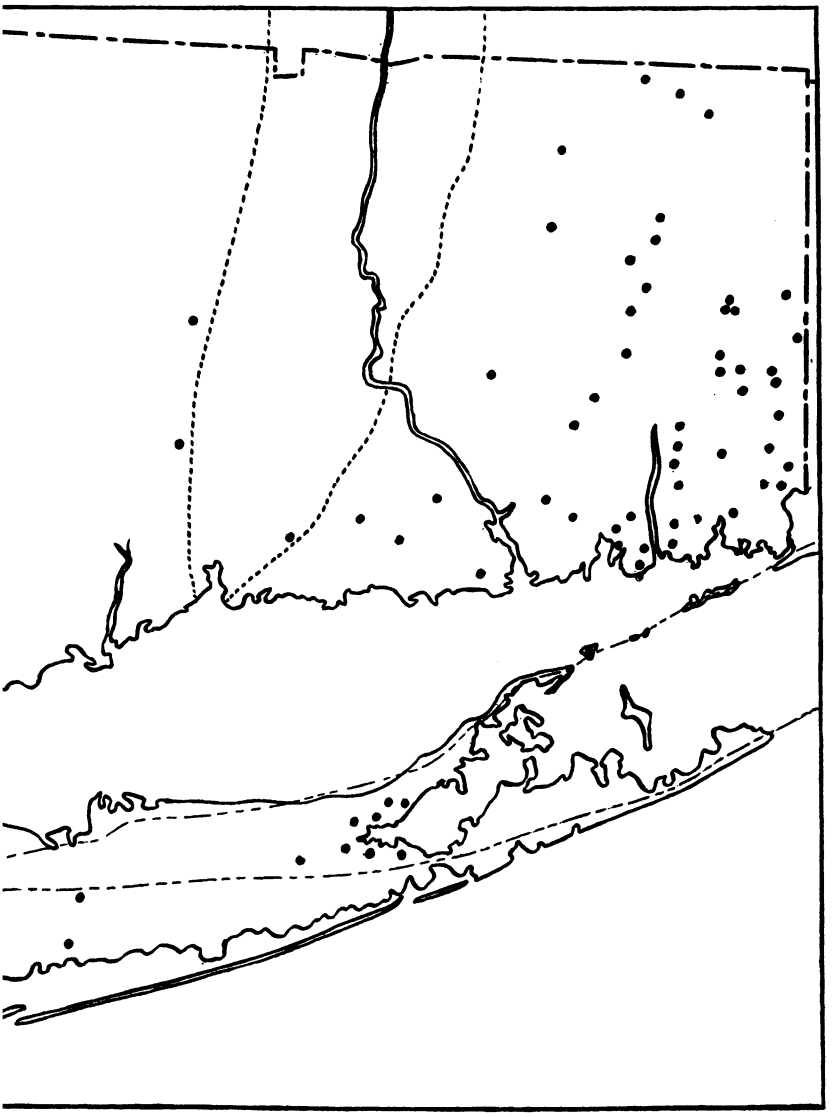


FIG. 2. Map of Connecticut and part of southern New York, showing location of ced and Lowland in Connecticut (-------), and position of Ronkokoma (—·—·—) and on Long Island.



ıthern New York, showing location of cedar swamps (●), boundaries between Highlands
ıition of Ronkokoma (——·——·——) and Harbor Hill (——·——·——·——) terminal moraines

Connecticut and then have vanished so completely from this region, leaving no evidence whatever of its passage—and this in spite of the frequency here of swamps in which edaphic conditions seem identical with those in swamps farther east where cedar abounds.

The possible relationship between cedar swamps and spruce bogs is also of interest. Swamps of the latter type, characterized in part by their relict northern flora, are widely scattered over the northern three quarters of the state, but with the exception of one small area where there are seven within the radius of a mile, are nowhere common. In the western half of the state there are upwards of twenty spruce bogs, while in eastern Connecticut only five are recorded—two of these within a few miles of the Connecticut River. The reason for their relative rarity eastward is suggested by conditions observed by the writer in two small swamps near Plainfield. Here the dominant trees are cedars, but interspersed among these are numerous straggling spruces. In a cedar bog at Bethany there are also said to be a few spruces, although the writer has been unable to locate them. It seems probable, therefore, that within comparatively recent geological times the spruce occupied many of the sites in eastern Connecticut which are now inhabited by the cedar; for, except in the northwestern highland, the spruce in this region seldom grows to a height of more than six meters and as a rule the trees form a very open stand, so that it would be a comparatively simple matter for invading cedars to secure a foothold and ultimately, by reason of their larger size and the dense shade produced by their close set crowns, to eliminate the former tenants.

Having outlined the role which certain historical factors have probably played in the origin and evolution of the plant life of Connecticut, there remains to be considered the manner in which coexisting forces influence the character of the flora. In the present paper only those phases need be treated which concern plant distribution in the large. The ultimate or climax formation attained in the region under surveillance, *i. e.*, the most mesophytic permanent type of vegetation which is capable of develop-

ment, is a forest composed largely of deciduous trees and hemlock. Considering this forest as a unit the following comprise the most important arborescent species:

Castanea dentata	*Liriodendron Tulipifera*
Quercus rubra	*Fraxinus americana*
Quercus alba	*Tilia americana*
Acer Saccharum	*Betula lutea*
Acer rubrum	*Pinus Strobus*
Fagus grandifolia	*Prunus serotina*
Tsuga canadensis	*Hicoria* sp.

But the forest is by no means uniform in structure throughout the state. Most widely disseminated and of greatest economic importance is the "sprout hardwood" type which represents the usual climax formation over fully five sixths of the state. This type of forest attains its highest development in the central lowland and along the coast, where it is dominated by chestnut, oaks, and red maple. The tulip tree is commoner here than elsewhere; *Ostrya virginiana* and *Cornus florida* are conspicuous secondary species; while *Hamamelis virginiana* and *Kalmia latifolia*—this latter the State Flower of Connecticut—are almost universally present. In eastern Connecticut the chestnut is of comparatively subsidiary importance, oaks being the dominant trees; the forest here is obviously less mesophytic than in the lowland and along the coast. But it is in the northwesten part of the state that the most mesophytic conditions prevail, and the climax forest here conforms with the "northern hardwood" rather than the "sprout hardwood" type. Here hemlock, beech, and sugar maple, together with yellow birch characterize the virgin woodland; (FIG. 3) *Acer pennsylvanicum* and *Acer spicatum* replace the hop hornbeam and dogwood; while, in addition to the omnipresent laurel, the undergrowth is made up very largely of *Viburnum alnifolium* and *Taxus canadensis*. To what degree these modifications in forest composition should be attributed to contemporaneous factors cannot be definitely decided. In a measure the presence or absence of particular species may be the result of geographic position, but it seems

more likely that their scarcity or abundance is determined by physiographic or climatic factors.

Owing chiefly to its geographical location and topographic diversity Connecticut may be regarded as a sort of transitional area between the north and the south where both boreal and austral

FIG. 3. Interior of virgin northern hardwood forest at Colebrook. Hemlock and beech with characteristic undergrowth.

forms can find favorable environmental conditions. This state represents the southernmost extent of range in the east,[1] so far as recorded, for nearly 70 plants of northward distribution, while about 80 species of southward range apparently reach here their northern limit in the east. As might be anticipated, the rugged highland regions possess a flora rich in boreal forms, while the preponderance of austral species is encountered long the coast and in the central lowland. From a phytogeographical standpoint three well defined centers of distribution within the state

[1] Some species which extend farther south along the mountains have been included in this estimate.

may be recognized. Reference has already been made to the southeastern center. Similarly the southwestern section may be looked upon as including the usual route along which northbound immigrants from the south today invade the state. It is in this area that *Melanthium latifolium*, *Liquidambar Styraciflua*, *Pyrus arbutifolia*, *Viburnum prunifolium*, *Crotonopsis linearis*, *Oenothera longipedicellata*, and *Cacalia suaveolens* reach their northern limit in the east; while many other species, such as *Wolffia columbiana*, *Aristolochia Serpentaria*, *Cimicifuga racemosa*, *Heuchera americana*, *Rubus cuneifolius*, and *Ilysanthes anagallidea*, which extend locally into other parts of Connecticut, are frequent or common here. Northwestern Connecticut, on the other hand, constitutes a natural center of distribution for boreal species. Mention has already been made of the nature of the climax forest in this region. The swamps, likewise, are suggestive of the north; for here, as nowhere else in the state, tamarack swamps are of frequent occurrence; while the spruce, elsewhere represented by dwarfed, scattered specimens, becomes in the bogs of northern Litchfield County a tree of goodly proportions, and in at least one locality forms a forest of appreciable extent. Furthermore, on the northern slopes of some of the higher mountains in this section spruces fifteen or more meters in height are sometimes found growing as upland mesophytes. The balsam fir (*Abies balsamea*) and arbor vitae (*Thuja occidentalis*) are also native at several stations in northwestern Connecticut. Altogether no less than 90 species of plants have been recorded *only* from this part of the state, and of these fully 30 per cent. reach here their southernmost limit of range in the east.[1] In the subjoined list are given a few of the seed plants which are apparently restricted to this area.

Cinna latifolia	*Mitella nuda*
Carex Bebbii	*Ribes prostratum*
Carex pauciflora	*Potentilla tridentata*
Carex paupercula	*Dalibarda repens*
Streptopus amplexifolius	*Viola nephrophylla*

[1] This estimate also includes some species which range farther south along the Alleghanies.

Habenaria macrophylla	*Epilobium palustre*
Spiranthes Romanzoffiana	*Vaccinium canadense*
Salix candida	*Galium trifidum*
Betula pumila	*Solidago uliginosa*
Ranunculus circinatus	*Petasites palmatus*

In addition to these three centers of distribution there are several other areas in which the character of the flora may similarly be ascribed to factors of more or less widespread influence. Foremost and most sharply delimited is the maritime province, which embraces the salt marshes and sea beaches. Salt marshes (Fig. 4), with their distinctive halophytic vegetation,

FIG. 4. Salt marsh at East Haven. Tidal creek in foreground.

are a familiar feature along the shore, developing behind barrier beaches or in sheltered inlets and frequently covering an area of several square miles. Along the Connecticut and Quinnipiac Rivers they extend inland a distance of six or eight miles, gradually merging into the fresh water swamps. Except for two shrubs

—*Iva oraria* and *Baccharis halamifolia*—all salt and brackish marsh species are herbaceous, and grass-like forms are predominant. The appended list includes some of the commoner representative species.

*Triglochin maritima**
Spartina glabra
Spartina patens juncea
*Spartina Michauxiana**
*Distichlis spicata**
Cyperus Nuttallii
*Eleocharis rostellata**
*Scirpus Olneyi**
Scirpus robustus
*Scirpus campestris paludosus**
*Juncus Gerardi**
*Atriplex patula hastata**
*Salicornia europaea**
Salicornia mucronata
Suaeda maritima
Limonium carolinianum
Gerardia maritima
Plantago decipiens
Solidago sempervirens
Aster tenuifolius
Aster subulatus
Pluchea camphorata

Along the sandy beaches which fringe the coast two classes of plants may be distinguished, viz., those able to grow in the more or less saline soil of the beach proper, and those restricted to the aeolian sands of the low dunes which usually cover the beach on its landward side. Peculiar to the beach itself are:

Atriplex arenaria
*Salsola Kali**
Arenaria peploides
*Cakile edentula**
*Euphorbia polygonifolia**
*Xanthium canadense**
Artemisia Stelleriana

Characteristic of the dunes are:

*Ammophila arenaria**
Panicum amaroides
Panicum oricola
Cyperus Grayii
*Myrica carolinensis**
*Prunus maritima**
*Lathyrus maritimus**
*Strophostyles helvola**
Lechea maritima
*Hudsonia tomentosa**
*Oenothera Oakesiana**
Solidago sempervirens

The ecological relations of the salt marsh and beach floras will be given more special treatment in a later paper, but it may be further noted here that not a few of the inhabitants of these areas

—*e. g.*, the species above marked with an asterisk—find a home in similar situations along the Great Lakes and westward.

There is still another group of plants, which are neither halophytic nor littoral but which, while frequent or common in the vicinity of the coast, rarely extend inland more than a few miles. Prominent among these are:

Woodwardia areolata	*Opuntia vulgaris*
Lycopodium inundatum Bigelovii	*Hottonia inflata*
Lilium superbum	*Rhexia virginica*
Iris prismatica	*Gerardia purpurea*
Habenaria ciliaris	*Eupatorium hyssopifolium*
Quercus stellata	*Artemisia caudata*

The cause of the coastward affinity in such plants is not wholly clear, but it should be pointed out that practically without exception the species concerned attain their optimum development farther south, while a large percentage of them are restricted to the Atlantic coastal plain, the Mississippi basin, and the region around the Great Lakes. Hardly less remarkable from a distributional standpoint is a second group of plants, also mainly southern in range, which are largely confined to the coast and to the valleys of the larger rivers. Representative of this class are:

Panicum virgatum	*Solidago odora*
Dioscoraea villosa	*Aster novi-belgii*
Cassia Chamaecrista	*Helianthus giganteus*
Onosmodium virginianum	*Bidens laevis*
Sicyos angulatus	*Bidens discoidea*

It seems probable that the limited distribution of these last two groups may in some way be associated with atmospheric conditions. There is an additional element in the river flora, however, whose presence is unquestionably due to edaphic rather than climatic factors. As illustrations, the cottonwood (*Populus deltoides*) and the silver maple (*Acer saccharinum*) may be selected. Although scattered locally throughout the state, it is only on the flood plains of the larger rivers that these two trees find conditions congenial to their optimum development. Here,

particularly along the Connecticut River, they form a conspicuous feature of the vegetation, frequently controlling large areas. Equally characteristic of—and where marked by an asterisk confined to—alluvial soil along the rivers are the following species:

Onoclea Struthiopteris
*Equisetum pratense**
*Equisetum palustre**
Equisetum fluviatile
*Equisetum variegatum Jesupi**
*Sagittaria arifolia**
Sagittaria heterophylla
*Cyperus erythrorhizos**
*Eleocharis diandra**
Eleocharis ovata
*Carex Grayii**
*Carex Tuckermani**
*Salix longifolia**
*Acer Negundo**
*Hypericum Ascyron**
Ambrosia trifida

In contrast to the plants in the two preceding lists it will be observed that more than half of the species here cited are boreal in their general distribution, no less than five reaching their southern limit in the east in Connecticut.

Although the primary object of the present paper is to describe some of the larger and more conspicuous features of plant distribution in this state, such an account would be incomplete without some mention of the eccentricities in range which are exhibited by certain species not heretofore noted. One of the best known examples of this sort is furnished by the persimmon (*Diospyros virginiana*), of which there is a well-established colony of more than 100 trees growing near the beach at Lighthouse Point, New Haven,—a station which was probably noticed as long ago as 1831[1] (Fig. 5). This tree has been found nowhere else in New England and the nearest locality to the south—in western Long Island—is fully 60 miles removed. An analogous case is afforded by the spike rush *Eleocharis quadrangulata*, which is abundant at West Pond, Guilford. Although the largest and most distinctive native species in the genus, no other station for it is known within a radius of 110 miles. Similarly, *Calliergon trifarium*, a handsome

[1] Howe, H. Catalogue of the phaenogamous plants and ferns growing without cultivation within five miles of Yale College, p. 13. New Haven, 1831. No definite station is given.

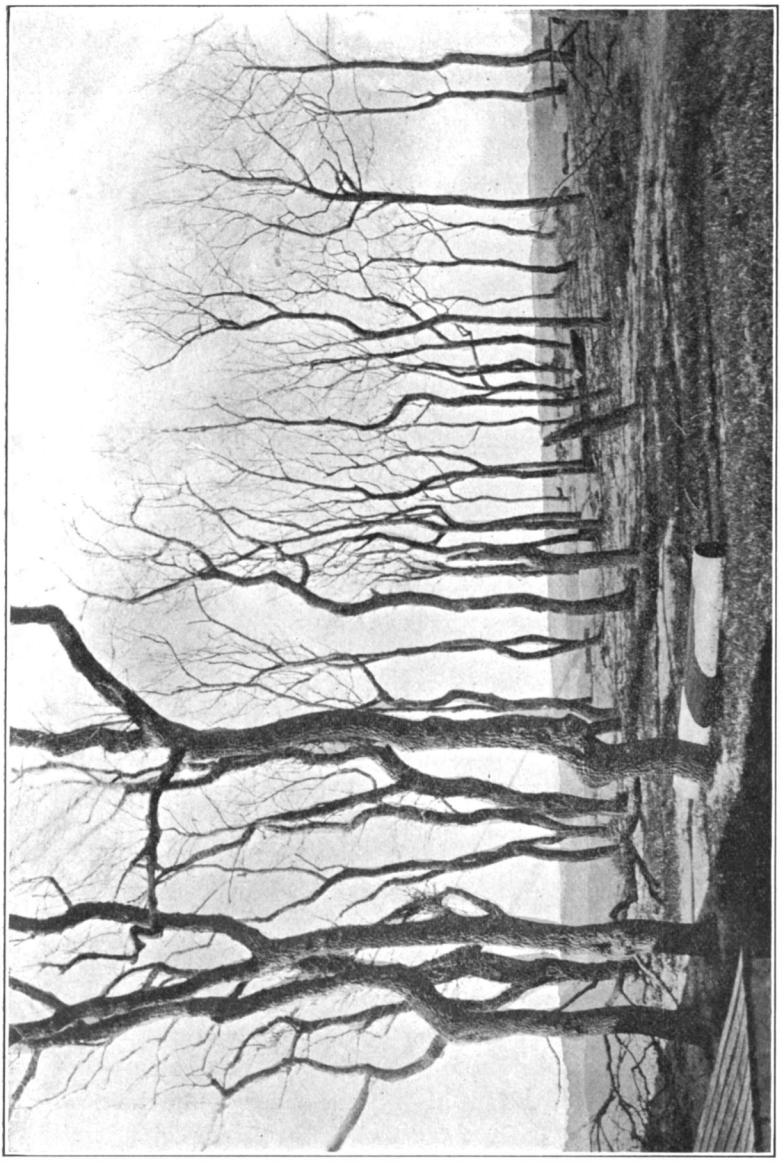


FIG. 5. Grove of persimmon (*Diospyros virginiana*) at Lighthouse Point, New Haven. Photograph taken about 1899 by Dr. W. E. Britton.

moss which is recognizable almost at a glance, grows luxuriantly in a bog at Salisbury but is reported from only six other North American localities, the nearest of which is more than 250 miles away. Another Connecticut moss, *Claopodium pellucinerve*, is apparently known elsewhere only from Yukon Territory and northern India. But even more puzzling are those cases where two species reach respectively their northern and southern limits at one and the same station. Three instances of this sort occur to the writer. In 1892 two ferns, *Cheilanthes lanosa* and *Cryptogramma Stelleri*, were collected on West Rock, a trap ridge near New Haven, where they grew side by side in crevices on the precipitous face of the rock. The first named species is widely distributed in the southern United States, but is unknown elsewhere in New England, the nearest recorded stations being along the Hudson River, more than 60 miles distant. The latter species is a northern calcicolous form which also occurs locally in the northwestern part of the state. Owing to the inaccessability of their eerie no one in recent years has ventured to ascertain whether this interesting station still exists. In a similar manner two mosses, *Pogonatum brachyphyllum* and *Aulacomnium androgynum*—the former a coastal plain form not otherwise reported north of southern New Jersey, the latter a boreal species which until recently had never been collected south of northern Massachusetts—grow on granitic ledges along the shore of Long Island Sound at stations less than a mile apart, while the two liverworts, *Anthoceros Macounii* and *Ricciella membranacea*, reach respectively their southern and northern limits in central Connecticut, where at Hartford they grow intermixed in the same ditch. No attempt is made to explain such anomalous vagaries of distribution. It would almost seem that the caprices of chance had overridden the natural laws of dissemination, and while edaphic factors may doubtless account for the persistence of a plant after it has once become established it is difficult to reconcile such antithetical associations as the last three above noted.

The chief factors which to-day control the distribution of the vegetation within the state may be summed up under two heads:

physiography and climate. From a geographical standpoint the state of Connecticut is naturally subdivided into three areas, viz., an eastern and a western highland and a central lowland. The boundaries of these divisions are roughly indicated on the accompanying map (fig. 2). The highlands, underlain by resistant granites, gneisses, and schists, contrast sharply with the lowland where the bed rock is composed largely of soft shales and sandstones. The contour of the highlands is for the most part rugged, but it is in the northwestern section of the state, among the southern Berkshires, that the greatest unevenness prevails. Elevations of 450 meters are common here, while there are several mountains over 600 meters in height. Not only do the greater altitude and the irregularity of the surface favor the presence in this latter region of northern plants but, as will be seen presently, these physiographic features are accompanied by climatic differences. In the lowland the surface is more nearly level, hills are frequent but high elevations are absent, while except along the two trap ranges, which traverse the region from north to south, precipitous cliffs and deep ravines, such as often abound in the highlands, are scarce. The contrast between highlands and lowland has even been accentuated by the activity of the glaciers; for in the former regions the debris deposited by the retreating ice sheet as a rule is heterogeneous and very unevenly distributed, while in the flatter lowland the till has been buried to a large extent beneath layers of stratified sands, gravels, and clays, so that the structure of the surface soil tends to be much more uniform. Among the most impressive features of the lowland, both from a physiographic and an ecological point of view, are the extensive sand plains—broad, level stretches which in places are utterly devoid of any but the sparsest and most xerophytic plant growth (Fig. 6). Such areas are usually populated by a flora which is preëminently southern in aspect, the northern element being correspondingly scarce. Other instances of a similar correlation between physiographic features and the character of the vegetation might be cited, but the discussion of these is better taken up later in connection with local problems.

Except in a superficial way little is known regarding the influence

of the chemical composition of the soil upon plant distribution. There are, however, quite a number of reputedly calcicolous

FIG. 6. Sand plains at North Haven. *Quercus ilicifolia* and clumps of *Andropogon scoparius* in foreground. In mid-distance an Andropogon "prairie" with scattered trees. View taken in March.

plants which in Connecticut would appear to be confined to the limestone areas in the western part of the state. Representative of these are:

Pellia Fabroniana
Lophozia badensis
Amblystegiella confervoides
Cratoneuron filicinum
Trisetum spicatum
Carex Crawei
Carex Castanea
Lobelia Kalmii
Arenaria stricta

Still other species, although not restricted to limestone, seem to be limited to calcium-containing substrata. Thus, *Grimaldia fragrans*, *Encalypta ciliata*, *Cryptogramma Stelleri*, *Asplenium Ruta-muraria*, *Carex eburnea*, and *Solidago squarrosa* have been found only in the limestone districts and on the trap ridges.

Although the existence of perceptible climatic differences within the state is unquestioned, it is as yet somewhat problematical to how great a degree the observed vegetational differences have been actuated by atmospheric factors. To a limited extent, however, it has been possible to coördinate more or less definitely with the phenomena of plant distribution meteorological data

relating to rainfall, evaporation, and temperature. In a series of experiments conducted during the past summer and described in detail elsewhere[1] it was demonstrated that, taking the ratio between the amount of water precipitated in the form of rain and that lost by evaporation as a criterion, there is a distinct correlation between the quantity of water theoretically available for plant use during the growing season and the distribution of forest types. In brief, it was found that while during the period of observation the rate of evaporation throughout the state far exceeded the rate of rainfall, there was an appreciable difference in the ratios between loss and gain in different regions. The estimated ratios were as follows: (*a*) western highland (interior) —.46; (*b*) central lowland (interior)—.35, coast—.36; (*c*) eastern highland (interior)—.31. These regions coincide approximately with (*a*) the northern hardwood area; (*b*) the sprout hardwood area dominated by chestnut; and (*c*) the sprout hardwood area dominated by oaks. Similarly temperature suggests a plausible explanation for the restriction of so many southern species to the immediate proximity of the coast, for while the length of the growing season in the interior averages 148 days, it is found that along the shore 177 days normally intervene between the last killing frost of spring and the first killing frost of autumn. It may be worthy of note also that in passing from east to west along the coast—from the shore of the ocean to the shore of Long Island Sound—there is a gradual diminution in the length of the season from 194 days at New London to 159 days at Norwalk. The longer growing season in southeastern Connecticut might be urged as a possible explanation for its peculiar flora, but an objection to such a view is the fact that over half of the plants noted above as *confined* to this section of the state have been found more than ten miles inland, notably at Voluntown where the growing season averages less than 140 days. The climate of northwestern Connecticut, on the whole, is cooler than elsewhere in the state, a fact which may be more or less intimately associated with the aspect of the vegetation there.

[1] Evaporation intensity as a determining factor in the distribution of vegetation in Connecticut. Botanical Gazette. In course of publication.

By way of summary it may be stated that the distributional phenomena herein described represent the cumulative effect of dynamic physical and chemical forces, some of which have long since become inactive while others continue to exert a modifying influence upon the physiognomy of plant life. In so far as they have either hindered or facilitated plant dissemination historical factors in a general way may be regarded as directly responsible for the composition of the local flora, while indirectly those glacial and preglacial forces which moulded the present physiographic features of the landscape still affect the character of the vegetation. To a very appreciable degree certain observed aspects of plant distribution are associated with contemporaneous conditions of topography, soil, and climate.

YALE UNIVERSITY.

SHORTER NOTES

BOTRYCHIUM OBLIQUUM AND VAR. DISSECTUM IN BERRIEN CO., MICHIGAN.—The seventh edition of Gray's Manual records these two plants as often occurring together in New England, New York, and Ohio. It may be of interest to note that they occur further westward, and possibly throughout the entire range of the typical form. October 19, 1912, in company with a class from the University of Chicago, I found several specimens of both growing together in an open wood near Sawyer. E. J. Hill in the *Fern Bulletin* for April 1912, states that both are found in Peoria Co., Ill., although he does not say that they are found together.

It is also of interest that while all the plants of the species were large and fertile (the spores not yet shed), those of the variety were only about one third as large, and consisted of the sterile segment only. It would appear from the specimens examined that *dissectum* is only a juvenile form of the species, but the material is too scanty to draw any conclusions as to this.

EDWIN D. HULL